The effect of photoperiod on the timing of spring migration in the Bewick's Swan

E. C. REES

Introduction

Since Baker (1938) first described the control of breeding seasons by ultimate and proximate factors, it has become well established that the timing of the migratory and reproductive cycles in birds are influenced by environmental conditions. Ultimate factors induce the development of particular behaviour patterns (e.g. the correspondence of the breeding season with optimal food supply) while proximate factors initiate and control physiological changes in a bird, so preparing it for migration or reproduction at the appropriate time. Daylength is a highly reliable indicator of changes in season, so has been adopted by many species as the proximal stimulus which determines the onset of the migratory cycle (Lofts & Murton 1968; Murton & Westwood 1977). The photoperiodic response may be modified, in the short term, by other environmental stimuli, but these usually work only in concurrence with appropriate photostimulation.

The Bewick's Swan (*Cygnus columbianus bewickii* is a wholly migratory species which visits Western Europe in winter and returns to the Siberian tundra north of the arctic circle to breed. Ultimate factors thought responsible for their moving to high latitudes include the emergence of protein-rich vegetation each spring and perhaps the availability of aquatic invertebrates needed for rapid growth of the young (Murton & Kear 1973). The reproductive and migratory cycles are closely linked as the swans must breed, moult, develop fat deposits and start their migration in just three to four months, while the tundra is habitable. These events may be governed by different endogenous clocks, each separately controlled by external stimuli, but daylength is the factor most likely to synchronize the cycles. The influence of photoperiod on the breeding season of waterfowl is clearly demonstrated by Murton & Kear (1978), who showed that a linear relationship exists between the mid-latitude of breeding range and onset of laying in many genera of Anatidae. Captive Bewick's Swans at the Wildfowl Trust, Slimbridge, follow this pattern in that they breed late compared with other species in the collection; some 15 hr of daylight seem necessary before they start to lay (Kear 1972; Murton & Kear 1973).

The importance of the short-term effects of climatic variations in inhibiting or stimulating bird migrations is emphasized by Nisbet & Drury (1968). Evans (1979a), studying variables thought to be involved on the days that Bewick's Swans arrive and depart from their wintering grounds, has found that large movements of swans are affected primarily by wind direction. Wind speed, rainfall, moon phase and associated cloud cover did not prove important variables. Temperature differences, although significant, were considered a reflection of the wind direction rather than having a direct influence on swan migration.

In a further paper Evans (1982) observed that Bewick's Swans wintering at Slimbridge departed much earlier than those from sites of similar latitude and suggested that this might be attributed to supplementary feeding under floodlights. However, the relationship between increased daylength and departure dates was not fully explored.

The Wildfowl Trust, Slimbridge, Gloucestershire provides unique facilities for a study of the effects of changes in photoperiod on the timing of spring migration in a wild population. This paper analyses Bewick's Swan departure patterns under different light regimes. The interaction between daylength, thought broadly to determine the migratory season and other modifying variables, thought to induce or inhibit departure from day to day, is investigated.

Study area

Since the mid-1950s the New Grounds, Slimbridge, Gloucestershire has become established as a major wintering site for Bewick's Swans, second only in Britain to the Ouse Washes on the Cambridgeshire/Norfolk border. In 1964, attracted by seven pinioned members of the species, wild Bewick's Swans started to frequent the Rushy Pen, an area of about three hectares including a shallow lake of

Wildfowl 33 (1982):119–32

half a hectare, inside the perimeter fence of the Wildfowl Trust, Slimbridge (P. Scott 1966; Evans 1978). The wintering population increased from 24 in 1963–1964 to a maximum count of 610 in 1978–1979, with some 300 swans regularly visiting the lake in mid-winter. Grain is provided several times a day and the birds are protected from disturbance. Two 1,500 w floodlights and nine 500 w floodlights illuminate one side of the lake at night (Figure 1).

Methods

A daily register of individual Bewick's Swans observed in the Rushy Pen has been maintained from the 1965–1966 winter onwards. Each swan is identified by its characteristic black and yellow bill pattern (Rees 1981). The number of swans visiting the lake is usually calculated from the total of individual swans registered daily. Counts of the population are also made to augment and confirm these figures. Discrepancies between the numbers identified and daily counts do occur, either when a large influx of swans causes recording problems or, towards the end of the season, when the swans spread out to graze in the surrounding fields and do not visit the Rushy Pen together. The highest figure is therefore taken as the most accurate count of swans in the area.

The number of days after 1 January on which 20%, 30%, 40%, 50%, 60%, 70% and 80% of the wintering population departs from Slimbridge has been determined from 1965–1966 to 1981–1982. The population is required to drop for three consecutive days for the departure to be considered genuine as the swans may have been inadequately observed on just one day. If the population increases again after a genuine departure is recorded, the first departure date is used. Influxes late in the season are probably due either to passage birds migrating from farther west or to birds returning after meeting inclement weather during the eastward journey. It is therefore thought that the initial decline in population does truly represent the onset of migration. In 1977–1978 the earlier of two departure patterns proved to be a large eastward movement. All the swans left Slimbridge by 6 February and 18 of these were identified in West Germany by 9 February. When the weather deteriorated later in the month, 14 of the swans identified in Germany returned to Slimbridge

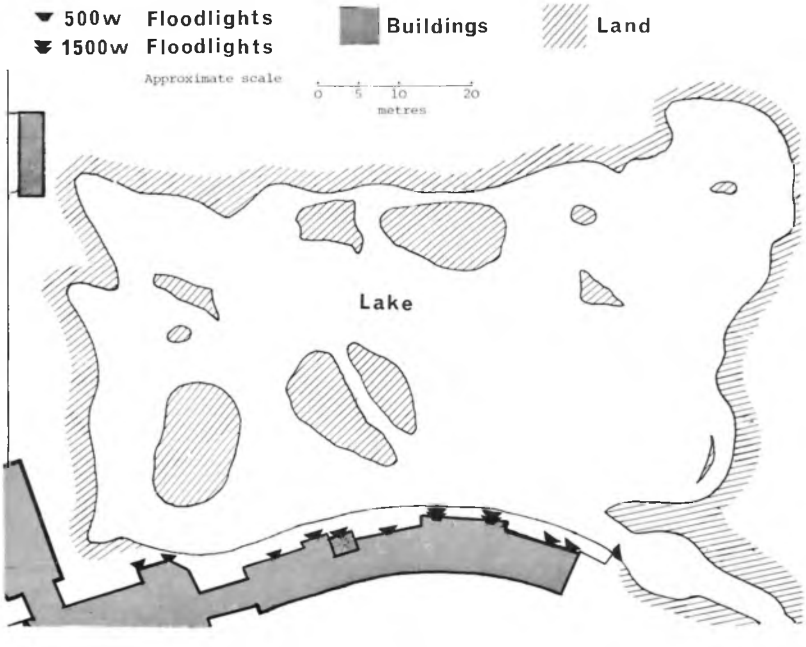

Figure 1. Sketch map of the main pond in the Rushy Pen and surrounding buildings, showing the position of the floodlights.

and one returned to Welney, Norfolk (Evans & Rees 1978; Evans 1982). There is no evidence for a major westward movement of swans leaving Slimbridge during the second half of the season. Records of swans identified in the same winter after departure from Slimbridge show that only one out of 458 birds resighted travelled west instead of east after 1 January (Evans 1982).

Floodlighting data

The floodlights were installed before Bewick's Swans started visiting the Rushy Pen. They were retained as the artificial illumination did not initially seem to affect the swans' behaviour or welfare. A comparison of the proportion of young among Bewick's Swans wintering at Slimbridge with those on the Ouse Washes showed that there was little difference in their reproductive success (Cadbury 1975; Evans 1979b).

Since 1965–1966 the majority of the Slimbridge-wintering swans have experienced three light regimes; natural daylength, illumination until 22.00 hr, and illumination until 20.00 hr.

(a) Natural daylength

From 1965–1966 to 1969–1970 the swans usually flew some 400 m to the Severn estuary to roost, departing soon after the feed provided at 16.00 hr. If they did remain in the pen overnight they slept around the far edge of the lake, out of the glare of the lights (Evans 1982). In 1968–1969 and 1969–1970 the swans were occasionally given grain under the floodlights, when the temperatures were low and numbers roosting in the pen were high, otherwise they remained undisturbed.

(b) Illumination to 22.00 hr

In 1970–1971 the swans started to anticipate the night-time feeds and waited for grain in front of the Honorary Director's house, which borders the SE end of the lake (see Figure 1). This area is well illuminated, so the swans were not only wakeful at night but were also subjected to floodlighting for long periods. Regular evening flights to the river did not occur until the second week in February.

In the first week of January 1972 the remains of 12 dead swans were found in the surrounding fields. Although the cause of death was not determined all had, to some extent, been eaten by foxes. Evans (1972) suggested that high tides may have forced the swans off the river onto dry land, where they were more vulnerable. It was therefore decided to encourage the swans to roost within the fox-proof perimeter fence and intensive feeding under floodlights was introduced. The regular night feeds reinforced the 'begging' behaviour recorded in 1970–1971, so from 1970–1971 to 1978–1979 the swans experienced a day up to six hours longer than the natural photoperiod. The floodlights were extinguished at 22.00 hr.

In 1971–1972 there was no floodlighting after 9 February due to the national fuel crisis. Natural daylength was taken as the photoperiod experienced by swans departing after this date. In 1973–1974 power cuts caused irregular floodlighting and records of the duration of illumination are incomplete. The 1973–1974 year is therefore excluded from these analyses.

(c) Illumination to 20.00 hr

In the preceding years it was noticeable that the swans were leaving on spring migration much earlier than they had previously. Therefore, from 1979–1980 to 1981–1982 the floodlights were faded out between 20.00 hr and 20.30 hr to see whether the reduced photoperiod delayed departure.

Feeding

Since the start of the study, the swans' natural diet, mainly of grass, has been augmented by wheat or barley distributed along two sides of the lake two or three times a day. The amount provided has greatly increased over the years, ranging from two barrow loads (at approximately 37 kg per load) each day in 1965–1966 to a maximum of 11 loads per day during the second week of January 1979, when climatic conditions were unusually severe. Since 1968–1969 varying distributions have also been made under evening floodlighting. The frequent feeding may result in Slimbridge swans developing fat deposits more rapidly than birds at an unprovisioned site, enabling the former to acquire suffient energy reserves for migration earlier. Some measure of physical condition and changes in the food supply should therefore be considered when determining which variables affect the timing of swan migration.

Evans & Kear (1978) found that on average the weights of Bewick's Swans at Slimbridge reach a peak in the second half of December, which suggests that they should be physically capable of migrating then. However, there are insufficient data to compare rates of weight gain in separate years or to study physical condition immediately before departure as only one or two catches of swans have been made each winter since 1974–1975. There is also no information on the rate of fat deposition in Bewick's Swans whose diet is not supplemented, as these birds have seldom been caught outside Wildfowl Trust centres.

In these analyses changes in the food supply must therefore be taken as an independent variable. Two separate subsections are used; the maximum number of daytime feeds and the maximum number of night-time feeds recorded each winter. In both cases the feeding pattern has to be established for at least a week before it is used. Unfortunately more precise data are not available. The weight of food issued to the Rushy Pen is rarely calculated and records of the number of barrows of grain distributed daily are incomplete. It would also be difficult to assess what quantity of grain the swans ingest and what proportion is eaten by the thousands of ducks present on the lake. However, as the food supply has increased so radically since 1965–1966, it is felt that even the generalized measure used may give interesting results.

Weather data

Daily records of wind direction, temperature and snowfall from 1965–1966 to 1980–1981 were obtained from the Meteorological Office at Gloucester, some 20 km from Slimbridge. Evans (1978) compared Gloucester weather data with information obtained from a small weather station established at the Wildfowl Trust in 1975–1976. The resultant observations proved to be similar and highly correlated, so justifying the use of Gloucester records in Slimbridge analysis.

As the Gloucester Weather Station closed in August 1981, weather data for 1981–1982 were obtained from Dursley, 8 km from Slimbridge (P. D. Bailey, pers. comm.).

To facilitate statistical analysis, weather conditions are divided into four major groups as described by Evans (1979a)

(1) North to East, 'Head' winds (340°–110°)
(2) South to West, 'Tail' winds (160°–290°)
(3) SE and NW, 'Side' winds (115°–155° and 295°–335°)
(4) Calm

If the wind blows in more than one direction each day, the most prevalent condition is used.

Disturbance

Bewick's Swans at Slimbridge are largely protected from disturbance, although noise or sudden movements in the buildings adjacent to the lake occasionally flush the birds. Catches of swans for ringing, also useful for gaining further information about the birds, and goose shoots in nearby fields, are more likely to encourage swans to leave the area. The effect that the frequency of these events has on swan departures was investigated.

Results

Bewick's Swan departure patterns under differing light regimes

The swan departure dates were divided into three groups according to the photoperiod experienced by the swans. The mean number of days after 1 January on which 20% to 80% of the population had departed was calculated for each group (Table 1).

A graph of the percentage of the population departed against departure date (Figure 2) shows three distinct regression lines corresponding to the three different light regimes. These suggest that the swans leave earlier in the season when subjected to an artificially long daylength. A Kruskal-Wallis one-way analysis of variance shows that the depature dates of the three groups differ significantly ($p < 0{\cdot}001$).

Extrapolation of the regression lines to the x axis gives the number of days after 1 January on which, apparently, the swans would first receive a daylength long enough to induce migration (Table 2). Therefore, swans illuminated until 22.00 hr should be ready to leave on 31 December, 17 days earlier than those lit until 20.00 hr and 58 days earlier than those under natural conditions. Natural daylength (sunrise to sunset) for each date plus the number of hours of artificial illumination received, gives the minimum photoperiod at which, theoretically, each of the three groups of swans were prepared to migrate (Table 2). The initial decline in numbers may, of course, be due partially to local dispersal rather than migration. However, Evans (1982) noted that swans from Slimbridge were identified in the same season at Welney, Norfolk, during the fourth quarter of December, so 31 December is not such an unlikely date for

Table 1. The number of days after 1 January on which 20% to 80% of the swan population had departed from Slimbridge under the three light regimes.

	Departure dates (Mean No. Days after 1 Jan.)		
% of Population departed	*A* Illumination to 22.00 hr (6 years' data)	*B* Illumination to 20.00 hr (3 years' data)	*C* Natural daylength (5 years' data)
20	9	27	63
30	17	32	64
40	19	35	67
50	22	47	68
60	27	49	69
70	36	51	73
80	38	51	75

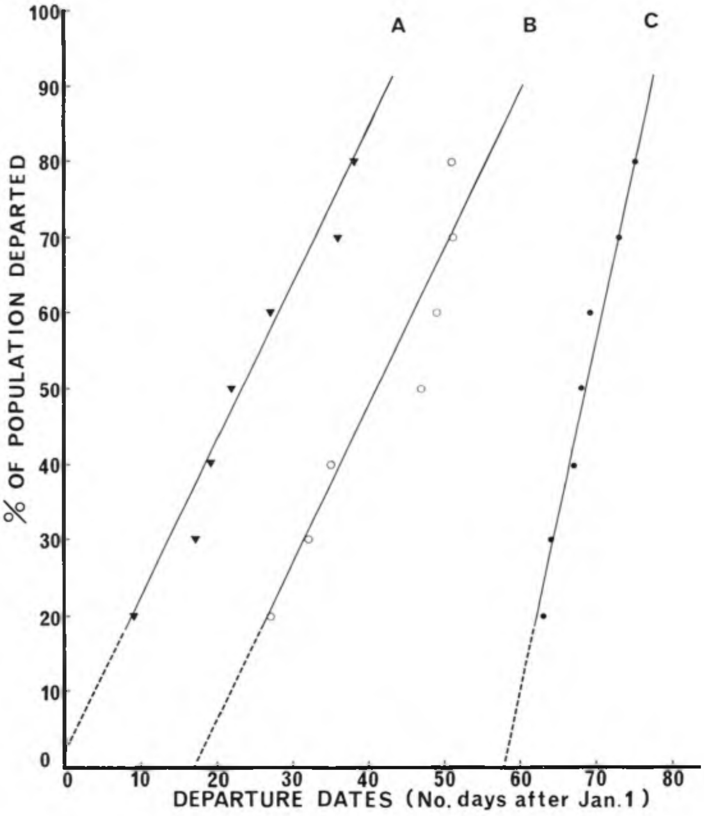

Figure 2. The relationship between the percentage of the swan population departed from Slimbridge and the number of days after 1 January for each of the light regimes. A = Illumination until 22.00 hr. B = Illumination until 20.00 hr. C = Natural daylength.

Table 2. The number of days after 1 January on which migratory activity apparently starts and the photoperiod received on these dates.

Daylength	Slope of regression line	No. of days after 1 Jan. on which swans should be ready to leave (i.e. × axis intercept)	Photoperiod at onset of migration (hr)
A Illumination to 22.00 hr	2·1	−1	13·73
B Illumination to 20.00 hr	2·0	17	11·87
C Natural daylength	4·9	58	10·75

the start of eastward migratory movement. Indeed one Slimbridge-wintering bird was sighted on the upper Elbe between West and East Germany as early as 28 December (Evans & Rees 1978; Evans 1982).

T-tests comparing the difference in slope of the three regression lines show that the rate of departure of swans exposed to a natural daylength is significantly greater than those that are floodlit both to 22.00 hr and to 20.00 hr ($p<0{\cdot}001$ in each case). There was no difference in the departure rates of the two illuminated groups (see Table 2). The slower decline in population when the swans leave earlier in the season and the corresponding increase in the photoperiod response threshold may, perhaps, be attributed to inhibitory effects of other environmental or physiological regulators.

The relative importance of different stimuli on the timing of the spring migration

The individual and combined effects of environmental variables on the Bewick's Swan departure dates were determined by Forward-step multiple regression analysis, following the method described in Draper & Smith (1966). Photoperiod, when considered alone, proved a significant influence on the timing of all but the 80% departure level (Table 3). However, the percentage variation in departure date which can be accounted for by changes in daylength declines substantially as the season progresses. It therefore seems that once the swans have received sufficient photostimulation to signal the start of the migratory season, other stimuli play an increasing role in regulating the timing of departure.

Weather data

The linear regression analyses gave dates on which the swans supposedly receive sufficient photostimulation to start their migration (see Table 2). Climatic conditions from these 'migration dates' to each departure level were analysed. The use of the 'migration date' as the start of the departure phase was considered appropriate as it is more likely to be of relevance to the birds than an arbitrary date such as 1 January.

(i) Wind direction

Variations in the proportions of the four wind conditions (Head, Tail, Side and Calm) from the migration date to the 20%, 50% and 80% departure dates did not have a significant effect on the timing of these departures (Table 4).

Table 3. The significance of photoperiod in regulating the onset of migration for a range of depature levels.

% of population departed	% of the variation in departure dates attributable to changes in daylength	Level of significance
20%	71·8	$p<0{\cdot}005$
30%	64·6	$p<0{\cdot}005$
40%	64·4	$p<0{\cdot}005$
50%	44·1	$p<0{\cdot}01$
60%	34·5	$p<0{\cdot}025$
70%	28·3	$p<0{\cdot}05$
80%	19·7	$p<0{\cdot}10$ Not significant

Daylength was then added to the regression so that the influence of wind direction might be re-examined, taking into account the variation in the departure dates caused by changes in photoperiod. The results of these analyses are listed in Table 5. Sequential F values cited in the table give the significance of each variable at the stage

Table 4. The influence of the four wind variables on departure dates.

% of population departed	Total % variation in departure dates accounted for by all four wind variables	Level of significance
20	23·3	p > 0·25 Not significant
50	15·5	p > 0·25 Not significant
80	22·7	p > 0·25 Not significant

Table 5. The influence of the four wind variables plus daylength on departure dates.

% of population departed	Variable (in order of incorporation into the regression analysis)	% variation in departure dates explained by the addition of each variable (cumulative)	Sequential F value	Final F value
20%	Daylength	71·8	35·69**	40·01**
	% Calm	77·0	2·95	2·48
	% Side	78·7	0·93	0·96
	% Head	80·9	1·28	3·54
	% Tail	84·7	2·47	2·47
30%	Daylength	64·6	25·58**	12·58**
	% Head	66·6	0·75	0·76
	% Tail	67·0	0·16	0·21
	% Calm	67·6	0·22	0·18
	% Side	67·6	0·01	0·01
40%	Daylength	64·4	25·30**	27·57**
	% Side	68·3	1·60	1·06
	% Calm	71·6	1·47	2·22
	% Tail	73·6	0·78	2·22
	% Head	77·0	1·50	1·50
50%	Daylength	44·1	11·03**	23·36**
	% Calm	54·4	2·93	8·11*
	% Tail	62·2	2·47	6·85*
	% Head	74·7	5·44*	4·45
	% Side	74·7	0·01	0·01
60%	Daylength	34·5	7·36*	9·93*
	% Head	47·0	3·08	4·23
	% Tail	53·3	1·60	2·42
	% Calm	57·1	0·97	1·02
	% Side	59·0	0·48	0·48
70%	Daylength	28·3	5·52*	15·14**
	% Head	48·2	5·00*	8·61*
	% Tail	61·7	4·22	4·94
	% Calm	67·1	1·81	1·70
	% Side	67·4	0·10	0·10
80%	Daylength	19·7	3·43	13·21**
	% Calm	44·9	5·95*	4·74
	% Head	52·6	1·96	5·58*
	% Tail	66·7	4·64	3·74
	% Side	66·7	0·01	0·01

D.F. for the Sequential F tests = (1,14) for the 1st variable, (1,13) for the 2nd, (1,12) for the 3rd, (1,11) for the 4th, (1,10) for the 5th.
D.F. for the Final F tests = (1,10) throughout.
* = significant at the 5% level. ** = significant at the 1% level.

that it is incorporated into the regression analysis; the final F values give the significance of each variable at the end of the procedure, allowing for the contribution made by all the other variables included. Differences between the sequential F and final F values show that in general the inclusion of the wind variables improves the overall significance of daylength (and vice versa) by their accounting for diverse features of the departure data. Indeed the significance of daylength is raised from $P<0{\cdot}05$ to $P<0{\cdot}01$ for 70% departed and $p<0{\cdot}1$ to $p<0{\cdot}01$ for 80% departed.

Photoperiod remains the most important influence on the timing of swan departures but the proportion of head winds, acting in concurrence with changing daylength, has a significant, inhibitory effect as the spring migration proceeds (Table 5). The percentage of days with no wind is taken as the best (i.e. most significant) single variable to succeed daylength in the regression analysis at the 80% departure level, but ultimately it proves less significant than the proportion of head winds. The head wind variable, though more highly correlated with departure dates, was not included earlier due to its relationship with other variables in the regression.

(ii) Temperature

Two measures of variation in temperature were used:

(a) The percentage of days with air frost from the migration date to the 20%, 50% and 90% departure levels and
(b) The mean daily minimum temperature recorded from the migration date to all eight departure levels.

The percentage of days of air frost, even when analysed with daylength and wind conditions, did not have a significant effect on the Bewick's Swan departure dates ($p>0{\cdot}05$). Only the two most influential wind conditions were used in each case as the others had proved of little importance.

The results obtained when the mean minimum temperature was analysed with daylength and the two most influential wind conditions are summarized in Table 6. Temperature had a significant effect on the 50% and 60% departures. The significant correlations found between changes in temperature and wind direction reflects the association between low temperatures and NE winds and between higher temperatures and south westerlies. These correlations could reduce the statistical significance of temperature as wind conditions might account for variations in the departure data which could be attributed to temperature. However, the low correlation between the mean daily minimum temperature and departure dates throughout the range indicates that temperature is not a prime long-term regulator (i.e. acting over several days or weeks) of Bewick's Swan departures from Slimbridge.

(iii) Snowfall and snowcover

It might be expected that both snowfall and snowcover would inhibit movement away from Slimbridge as the swans would be more dependent on the provision of grain

Table 6. The interaction between mean minimum temperature, % head winds, % tail winds and departure dates.

% of population departed	Correlation between mean minimum temperature and: % head winds	% tail winds	departure dates	Sequential and final F values for MMT
20	−0·60*	—	0·07 NS	0·15 NS
30	−0·59*	0·72**	−0·01 NS	0·52 NS
40	—	0·67**	−0·07 NS	3·34 NS
50	—	0·71**	−0·20 NS	11·91**
60	−0·60*	0·74**	−0·29 NS	5·64*
70	−0·63**	0·71**	−0·17 NS	1·77 NS
80	−0·53*	—	−0·09 NS	0·39 NS

DF = 1,10 for the F tests and 1,14 for the correlations.
* = F value significant at 5% level.
** = F value significant at 1% level.
NS = Not significant.
— = Shows that the wind condition has been omitted.

under these conditions. However, neither variable had a significant long-term effect on the regulation of departure dates, probably because snow did not persist for more than eight consecutive days between 1965–1966 and 1981–1982. When the percentage of days with snowfall was analysed in relation to daylength and the two most significant wind conditions, its F values were 2·52 ($p > 0{\cdot}05$) at the 20% departure level, 0·21 ($p > 0{\cdot}05$) at the 50% departure level and 0·31 ($p > 0{\cdot}05$) at the 80% departure level. The percentage of days on which snow lay to a depth of more than 0·5 cm were similarly analysed and its F values were 0·30 ($p > 0{\cdot}05$), 3·91 ($p > 0{\cdot}05$) and 0·37 ($p > 0{\cdot}05$) respectively.

Feeding

The effect that increased day feeds, night feeds and daylength have on the timing of Bewick's Swan departures was investigated at the 20%, 50% and 80% departure levels. Daylength proved the most statistically significant variable at the 20% level, but was superseded by the number of night feeds at the 50% and 80% levels, with sequential F values of 13·20 ($p < 0{\cdot}01$) and 14·88 ($p < 0{\cdot}01$) respectively. However a very high correlation exists between night feeds and photoperiod (Table 7) as it was the introduction of regular night feeding that encouraged the swans to loiter under the floodlights. It is therefore difficult to establish the relative importance of the two variables, particularly as the maximum number of night feeds is a very rough measure of the quantity of food distributed.

However, when day and night feeds are consolidated the total increase in food supplied proved less significant than photoperiod in determining the onset of swan migration (Table 8). Feeds appeared more significant only at the 80% departure level. Moreover, the high but spurious correlations between feeds and daylength mean that a substantial correlation would be expected between feeds and departure dates (− 0·41 at the 50% departure level) irrespective of any interaction between these variables (Table 8, column D). The low residual correlation (column E) suggests that feeding has little effect on swan departures. Fisher Z-tests reinforce this view by demonstrating that there is no

Table 7. The interaction between the number of day feeds, the number of night feeds, daylength and departure dates.

% of population departed	Correlation between night feeds and daylength	Correlation between night feeds and departure date	Correlation between day feeds and departure date	Correlation between daylength and departure date
20	0·58*	−0·74**	−0·63**	−0·85**
50	0·76**	−0·70**	−0·51*	−0·66**
80	0·66**	−0·72**	−0·46 NS	−0·44 NS

* = significant at the 5% level. ** = significant at the 1% level. NS = Not significant.

Table 8. The interaction between the total number of feeds, daylength and departure dates.

% of population departed	*A* Correlation between daylength and departure dates	*B* Correlation between total no. of feeds and departure dates	*C* Correlation between daylength and total no. of feeds	*D* Product of correlation between A & C	*E* Residual correlation between feeds and departure dates
20	−0·85**	−0·69**	0·53*	−0·45	−0·40
30	−0·80**	−0·60*	0·56*	−0·45	−0·40
40	−0·80**	−0·60*	0·55*	−0·44	−0·36
50	−0·66**	−0·58*	0·62*	−0·41	−0·25
60	−0·59*	−0·51*	0·67**	−0·40	−0·19
70	−0·53*	−0·54*	0·64**	−0·34	−0·19
80	−0·44 NS	−0·55*	0·61*	−0·27	−0·17

* = significant at the 5% level. ** = significant at the 1% level. NS = not significant.

significant difference ($p > 0{\cdot}05$) between the calculated correlation of feeds with departure dates (column B) and their anticipated correlation (column D).

It might be argued that the number of feeds is the influential variable rather than daylength. However, several papers show that the weights of migrant waders and waterfowl peak shortly after arrival at the wintering grounds (Elder 1946; Matthews & Campbell 1969; Owen & Cook 1977; Pienkowski *et al.* 1979; Owen 1981), which suggests that some variable other than condition must regulate departure. Food shortage may, of course, inhibit departure under exceptional circumstances, but these are not considered here.

It is interesting to note that the increase in the total number of feeds is less highly correlated with swan departures than the number of night feeds, particularly as the range of the former is 2 to 13 while the range of the latter is only 0 to 2. This strongly suggests that the *effect* that night feeding has in persuading the swans to stay under the lights is the important factor, rather than the extra quantity of food provided.

Disturbances

The small number of goose shoots and swan catches held from the theoretical migration date to the day on which 50% of the population departed did not prove a significant influence on the timing of 50% departures from Slimbridge. When analysed with daylength, $F = 1{\cdot}06$ ($p > 0{\cdot}05$) for shoots and $F = 1{\cdot}83$ ($p > 0{\cdot}05$) for catches. The combined effect of the two disturbances was also insignificant, $F = 2{\cdot}60$ ($p > 0{\cdot}05$).

It seems likely that efforts made to keep both shoots and swan catches to a minimum has limited the effect of these events.

Population size

Annual fluctuations in the size of the population, represented by the maximum count recorded each winter, and yearly changes in the proportion of young recorded at Slimbridge were not significantly related to variations in departure dates ($F = 0{\cdot}07$, $p > 0{\cdot}05$ for size of population and $F = 0{\cdot}75$, $p > 0{\cdot}05$ for percentage young when each variable was analysed with daylength at the 50% departure level).

A comparison of Slimbridge departure patterns with those at Welney, Norfolk, and Wexford, Eire

The effect that floodlighting has on the timing of Bewick's Swan migration may also be investigated by comparing the departure patterns of Slimbridge birds with those wintering under more nature conditions. Two suitable sites, which hold similar numbers of swans to Slimbridge and are regularly observed, are the Wexford Wildfowl reserve in Eire and Welney Wildfowl refuge, Norfolk.

The establishment of the Wexford Wildfowl reserve in 1969, combined with the discovery by the swans that root crops are palatable, resulted in a marked increase in the Bewick's Swan population at this site. Numbers on the North and South Slobs rose from 43 in 1968–1969 to 154 in 1969–1970 and 439 in 1970–1971. In 1978 the growing of root crops was discontinued so swans that arrived in the autumn quickly dispersed (O. J. Merne, pers. com.). Only data from 1969–1970 to 1977–1978 was therefore used. Little movement was noted between the two slobs so their counts were combined to give the total number present in the area.

In 1971–1972 the Wildfowl Trust started distributing grain two or three times a day in front of the observatory at Welney, Norfolk, which attracted substantial numbers of swans from the rest of the Washes (D. K. Scott 1978). The lagoon there has been floodlit until 19.30 hr each evening since 1970–1971 and the last feed takes place under the lights at around 18.30 hr. A daily register of up to 450 individual Bewick's Swans frequenting the lagoon was made in 1974–1975, 1975–1976 and 1980–1981. Fluctuations in the number of swans recorded is thought to reflect changes in the total number of swans in the Welney area (D. K. Scott, pers. com.). Swans visiting Welney after wintering at Slimbridge were not included in the Welney counts as they were considered to be already on migration.

The number of days after 1 January on which counts at Wexford and numbers identified at Welney first dropped below a range of percentages of the season's maximum was calculated. The mean date for each departure level was obtained for each site and compared with departures from Slimbridge under the 22.00 hr and 20.00 hr light regimes (Table 9 and Figure 3).

Mann-Whitney U-tests show that there is no significant difference between departures from Welney and Wexford or between the departures from Welney and Slimbridge when lit until 20.00 hr $(p > 0{\cdot}05)$. Both the Wexford and Welney populations departed significantly later than Slimbridge swans when the last were illuminated until 22.00 hr $(p < 0{\cdot}001)$. Wexford swans also departed later than Slimbridge birds lit until 20.00 hr $(p < 0{\cdot}05)$.

It might be expected that Bewick's Swans wintering in Ireland would start their eastward migration before, or at least at the same time as those wintering at

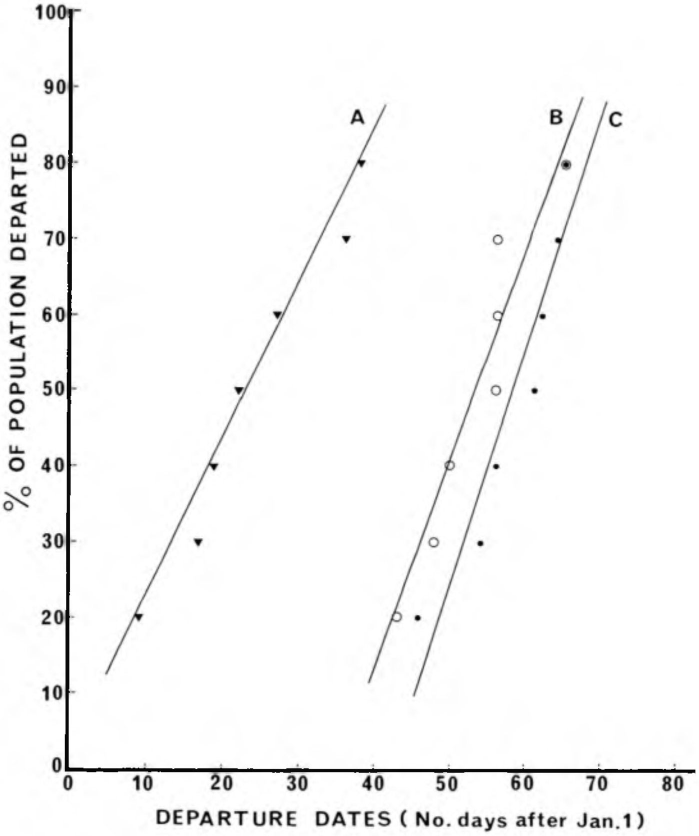

Figure 3. Departure patterns of Bewick's Swans at different sites. A = Slimbridge (floodlit until 22.00 hr). B = Welney. C = Wexford.

Table 9. The number of days after 1 January on which 20% to 80% of the swan population had departed from Slimbridge, Welney and Wexford.

	Departure dates (Mean no. of days after 1 January)			
% of population departed	Slimbridge floodlit till 22.00 hr (6 years' data)	Slimbridge floodlit till 20.00 hr (3 years' data)	Welney (3 years' data)	Wexford (9 years' data)
20	9	27	43	46
30	17	32	48	54
40	19	35	50	56
50	22	47	56	61
60	27	49	56	62
70	36	51	56	64
80	38	51	65	65

Slimbridge. However, these results reinforce the findings of Evans (1982), who observed that the average 50% departure from Wexford was significantly later than 50% departure from Slimbridge between 1969–1970 and 1977–1978. This could be attributed to the floodlighting at Slimbridge, although there has been no control for other variables.

It is not altogether surprising that there is no significant difference in the mean departure dates of Welney swans and those at Slimbridge under the 20.00 hr light regime, as the Slimbridge birds receive just 30 min extra floodlighting each night. However, when the Slimbridge swans were exposed to an extra 2½ hours photostimulation, they left significantly earlier. It is not known whether Bewick's Swans frequenting the lagoon at Welney leave earlier than, or at the same time as, swans on the rest of the washes. If they leave earlier, it would suggest that, although the area is more open than at Slimbridge, the swans there still receive sufficient photostimulation to advance their migration. Figure 3 indicates that this may occur as Welney swans start leaving slightly earlier than Wexford birds, despite being some 350 miles farther east. However, if there is no difference between the departure pattern of swans at Welney and those on the surrounding fens, it suggests that late February may be the natural time for 50% of most of the British wintering population to start on migration as there was no significant difference in the timing of departures from Wexford and Welney.

Discussion

Changes in the duration of artificial floodlighting experienced by the Bewick's Swan population at Slimbridge had a significant effect on the timing of their departures. This complies with the classical view that photoperiod is one of the main factors regulating physiological and behavioural cycles, including migration. There is no evidence to suggest that the swans are affected by a return to a natural photoperiod on leaving Slimbridge. It seems likely that, once triggered, the migratory activity persists unless the migrants encounter adverse weather conditions (as in Evans & Rees 1978).

It is also demonstrated that increases in daylength become progressively less important in inducing migration while the relative significance of wind direction (particularly North to East 'head' winds) in regulating departure dates increases. Therefore, once the swans have received sufficient photostimulation to determine the onset of the migratory season, the final departure date is modified by wind conditions.

Since 1978–1979 a small group of up to 15 swans have chosen to winter in a separate pen within the enclosures at the Wildfowl Trust, Slimbridge, where they were fed twice a day but were not exposed to floodlighting. While firm conclusions should not be drawn from the activities of a self-selected population, the late departure of these birds each season does further suggest the involvement of daylength in controlling migration. From 1978–1979 to 1980–1981 inclusive they left during the first week of March (60 to 67 days after 1 January) and in 1981–1982 they left on 28 February (day 59), average departure dates for birds receiving a natural photoperiod (Table 2).

This study has described the proximate factors responsible for the timing of departure of the Bewick's Swan population as a whole, but has not explored those factors which may influence the movements of individual birds. Baker (1978) gives several examples of variations in the migration threshold of migrants and non-migrants of the same species. The variations are explained by geographical, sexual and ontogenetic differences. Differences in individual migration thresholds may also occur within the Bewick's Swan population, which would explain the swans' failure all to leave on the same day. Variables which might influence the threshold level from year to year include sex, age, the number of days spent at Slimbridge, experience of the site, reproductive history, social class and social status. Indeed Evans (1980) has already shown that experienced birds tend to stay longer than birds new to Slimbridge. However, a genetic component, which fixes the migration threshold, may also be involved. An investigation of the departure patterns of individual swans in successive years would show whether certain birds tend always to leave late and whether an innate response threshold is modified by other variables.

Prolonged photostimulation has been shown to precipitate early migration but, as yet, there is no evidence to suggest that premature departure is damaging to the swans. The migration and reproductive cycles are closely linked, though not necessarily regulated by the same control mechanisms, yet when Slimbridge birds reversed their spring migration in February 1978 (Evans & Rees 1978) their subsequent breeding season proved no less successful than that of the rest of the population. Nine of the 18 swans identified on the continent by the end of the first week in February were resighted in 1978–1979. One pair returned with a cygnet (i.e. 11·1% young among the returnees) after a generally poor breeding season (8·7% juveniles registered at Slimbridge and 8·0% counted on the Ouse Washes, D. Salmon pers. com.). It must still be open to debate, however, whether interference with the swans' natural cycles is more generally detrimental to their wellbeing, particularly in view of the unnecessary flight and energy expenditure involved in a reversed migration.

Acknowledgements

I am particularly grateful to Dr C. H. Tuite and Dr J. M. V. Rayner for writing computer programmes which facilitated analyses of the data. I would also like to thank Dr M. Owen for advice on the interpretation of the statistics, O. J. Merne and E. P. Kingston for providing the Wexford data, Dr D. K. Scott for information from Welney, the staff at the Gloucester Meteorological Office, who kindly made their records available, P. D. Bailey for the 1981–1982 weather data and R. H. J. Graham for constructive discussions on ideas and text. Professor G. V. T. Matthews made helpful comments on a draft of the paper.

Summary

Bewick's Swans *Cygnus columbianus bewickii* floodlit from duck until 22.00 hr started their spring migration significantly earlier than birds illuminated until 20.00 hr; these latter, in turn, left before those receiving a natural photoperiod. The effects of variations in wind conditions and temperature and of snowfall, snowcover and disturbances, were also considered, but only the proportion of days with North to East ('head') winds had a significant influence on the departure pattern. In the case of food supplied to the birds the relevant factor was thought to be timing rather than the quantity of grain provided.

References

Baker, J. R. 1938. The relation between latitude and breeding seasons in birds. *Proc. Zool. Soc. Lond.* 108: 557–82.

Baker, R. R. 1978. *The evolutionary ecology of animal migration.* London: Hodder & Stoughton.

Cadbury, C. J. 1975. Populations of swans at the Ouse Washes, England. *Wildfowl* 26: 148–59.

Draper, N. R. & Smith, H. 1966. *Applied regression analysis.* London: J. Wiley & Sons.

Elder, W. H. 1946. Age and sex criteria and weights of Canada Geese. *J. Wildl. Manage.* 10: 93–111.

Evans, M. E. 1972. Slimbridge: the wild swans 1971–72. *Wildfowl* 23: 132–5.

Evans, M. E. 1978. Some factors influencing the use of a wintering site by Bewick's Swans, studies through individual identification. M.Sc. thesis, University of Wales.

Evans, M. E. 1979a. The effects of weather on the wintering Bewick's Swans *Cygnus columbianus bewickii* at Slimbridge, England. *Orn. Scand.* 10: 124–32.

Evans, M. E. 1979b. Aspects of the life cycle of the Bewick's Swan, based on recognition of individuals at a wintering site. *Bird Study* 26: 149–62.

Evans, M. E. 1980. The effects of experience and breeding status on the use of a wintering site by Bewick's Swans *Cygnus columbianus bewickii. Ibis.* 122: 287–97.

Evans, M. E. 1982. Movements of Bewick's Swans, *Cygnus columbianus bewickii*, marked at Slimbridge, England from 1960 to 1979. *Ardea* 70: 59–75.

Evans, M. E. & Kear, J. 1978. Weights and measurements of Bewick's Swans during winter. *Wildfowl* 29: 118–22.

Evans, M. E. & Rees, E. C. 1978. Slimbridge: the wild swans 1977–78. *Wildfowl* 29: 166–7.

Kear, J. 1972. Reproduction and family life. Pp. 79–124 in *The Swans* by P. Scott and the Wildfowl Trust. London: Michael Joseph.

Lofts, B. & Murton, R. K. 1968. Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. *J Zool. Lond.* 155: 327–94.

Matthews, G. V. T. & Campbell, C. R. G. 1969. Weights and measurements of Greylag Geese in Scotland. *Wildfowl* 20: 86–93.

Murton, R. K. & Kear, J. 1973. The nature and evolution of the photoperiodic control of reproduction in wildfowl of the family Anatidae. *J. Reprod. Fert., Suppl.* 19: 67–84.

Murton, R. K. & Kear, J. 1978. Photoperiodism in waterfowl: phasing of breeding cycles and zoogeography. *J. Zool. Lond.* 186: 243–83.

Murton, R. K. & Westwood, N. J. 1977. *Avian breeding cycles.* Oxford: Univ. Press.

Nisbet, I. C. T. & Drury, W. H. 1968. Short-term effects of weather on bird migration: a field study using multivariate statistics. *Anim. Behav.* 16: 496–530.

Owen, M. 1981. Abdominal profile—a condition index for wild geese in the field. *J. Wildl. Manage.* 45: 227–30.

Owen, M. & Cook, W. A. 1977. Variations in body weight, wing length and condition of Mallard *Anas platyrhynchos platyrhynchos* and their relationship to environmental changes. *J. Zool. Lond.* 183: 377–95.

Pienkowski, M. W., Lloyd, C. S. & Minton, C. D. T. 1979. Seasonal and migrational weight changes in Dunlins. *Bird Study* 26: 134–48.

Rees, E. C. 1981. The Recording and retrieval of bill pattern variations in the Bewick's Swan. *Proc. IWRB Symp. Sapporo*: 105–19.

Scott, D. K. 1978. Social behaviour of wintering Bewick's Swans. Ph.D. thesis, University of Cambridge.

Scott, P. 1966. The Bewick's Swans at Slimbridge. *Wildfowl Trust Ann. Rep.* 17: 20–26.

E. C. Rees, The Wildfowl Trust, Slimbridge, Gloucester, GL2 7BT.

Bewick's Swans feeding under floodlights at Slimbridge (*Philippa Scott*).